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MATING AND SELF-BURYING BEHAVIOR OF *HOMALONYCHUS THEOLOGUS* CHAMBERLIN (ARANEAE, HOMALONYCHIDAE) IN BAJA CALIFORNIA SUR

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ABSTRACT. The spider *Homalonychus theologus* is endemic to desert zones from southwestern California to southern Baja California Peninsula. Until now little has been published about its biology. In this paper we describe the reproductive and self-burying behavior and some aspects of the ecology of the species. Courtship behavior is between levels I and II, and the copulation position is a modification of type III. The male wraps the female's legs in silk before mating. This behavior could help justify inclusion of the Homalonychidae in the superfamily Lycosoidea. Possible camouflage behavior was attributed to the observation that these spiders can camouflage themselves by adhered sand grains to their bodies and buried themselves in the substratum. Females constructed eggsacs two days on average after mating one eggsac contained 29 eggs and other zero. Females incorporated sand ''collars'' to the egg sac with silk, probably as protection for the eggs against the dry environment as well as camouflage. This activity was carried out within 34 hours before oviposition. In the field, solitary spiders were found mainly under dead fallen cacti *Pachycereus pringlei*.

RESUMEN. La araña *Homalonychus theologus* es endémica de las zonas desérticas del sur de California hasta el sur de la península de Baja California. Hasta ahora se conoce poco acerca de su biología. En este artículo describimos los hábitos reproductores, conducta de enterramiento y aportamos algunos datos ecológicos de esta especie. La conducta de cortejo es intermedia entre los niveles I y II y la posición de cópula corresponde a una modificación del tipo III. El macho envuelve las patas de la hembra con seda antes de la cópula. Esta conducta puede contribuir a que las Homalonychidae puedan ser incluidas en la Superfamilia Lycosoidea. La posible conducta de enterramiento fue registrada cuando las arañas incorporaron granos de arena a sus cuerpos y se enterraron en el sustrato. Las hembras fabrican sus ovisacos pocos días después del apareamiento con un promedio de dos días en su elaboración y el número de huevos observado fue de 0–29 por ovisaco. Las hembras incorporan ''collares'' de arena con seda al ovisaco como una probable protección de los huevos a la desecación del medio. Este evento fue llevado a cabo en 34 horas. En el campo, las arañas se encontraron principalmente solas y bajo cardones en descomposición *Pachycereus pringlei*.

Keywords: *Homalonychus*, Baja California, mating behavior, self-burying behavior

Homalonychus theologus Chamberlin 1924 is one of two homalonychid species endemic to North America. This family is distributed in the warm deserts of southwestern United States and northwestern Mexico (Gertsch 1979; Roth 1984). *Homalonychus theologus* is found from southern California to southern Baja California Peninsula, on the adjacent islands Cedros and Margarita in the Pacific Ocean, and on several islands in the Gulf of California (Roth 1984); it is considered endemic to these regions.

Homalonychids are wandering spiders usually found in fine sand or soil, under loose boulders, boards or detritus. Only females and immatures cover their bodies with fine soil, which adheres to the setae of their integument (Roth 1984). *Homalonychus theologus* may mimic dry cactus spines by joining their legs in pairs as a potential defensive response.

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They cover the egg sacs with fine sand, probably to avoid predation (Vetter & Cokendolpher 2000).

Although *H. theologus* appears to be one of the most numerous spiders in the Baja California Peninsula and adjacent islands (Roth 1984), only one short paper (Vetter & Cokendolpher 2000) focused on the biology of this species, and another on the taxonomy of the family Homalonychidae (Roth 1984) has been published. In this paper, we examine mating and self-burying behavior of *H. theologus*.

METHODS

Spiders were collected at two sites in the Cape region of southern Baja California Peninsula: El Comitán and San Pedro, located at 24°08′7″N, 110°25′52″W and 23°54′44″N, 110°15′8″W, respectively. The local climate is very dry to semidry with rain in summer only and median annual temperatures from 22–28 °C (García 1973). Vegetation is sarcocaulescent scrub consisting mostly of ''cardón'' *Pachycereus pringlei* and ''cholla'' *Opuntia cholla* (León de la Luz et al. 1996).

Collections were taken weekly in El Comitán from 1200–1400 h, from August 2000–June 2001. Spiders were collected by hand from under decaying cardons and other cacti. Each spider was transported individually in a 250 ml plastic jar to the laboratory. Voucher specimens of *H. theologus* were deposited in the arachnid collection of the CIBNOR.

In San Pedro, spiders were collected in August, October and November 2000, and January 2001 for behavior observations under laboratory conditions. The microhabitat of spiders at both sites was described, and the number of specimens captured at each site was recorded. A total of 57 immature and adults were maintained in the laboratory and were used for behavior studies. Spiders were kept always in a dark 1.87 × 2.00 m room with temperature 23–27 °C and relative humidity 50–60%. Observations of mating behavior were made from 6 March–17 April 2000 between 1000–1300. Sixteen male/female pairs were used. Females were introduced to a 22.7 × 20.5 cm glass container at 26.2 °C and 46.8% relative humidity with fine soil as a substrate; males were introduced 1 hr later; each pair was permitted to mate, after which females were placed individually in transparent 250 ml plastic jars. Fine soil was placed in the bottom of each jar as substrate, with a piece of dry cactus as retreat and a small container of wet cotton for water. Each jar was covered with fine weave cloth. Mating time was recorded. If a pair didn't mate within 10 minutes, one of the pair was replaced by another of the same sex.

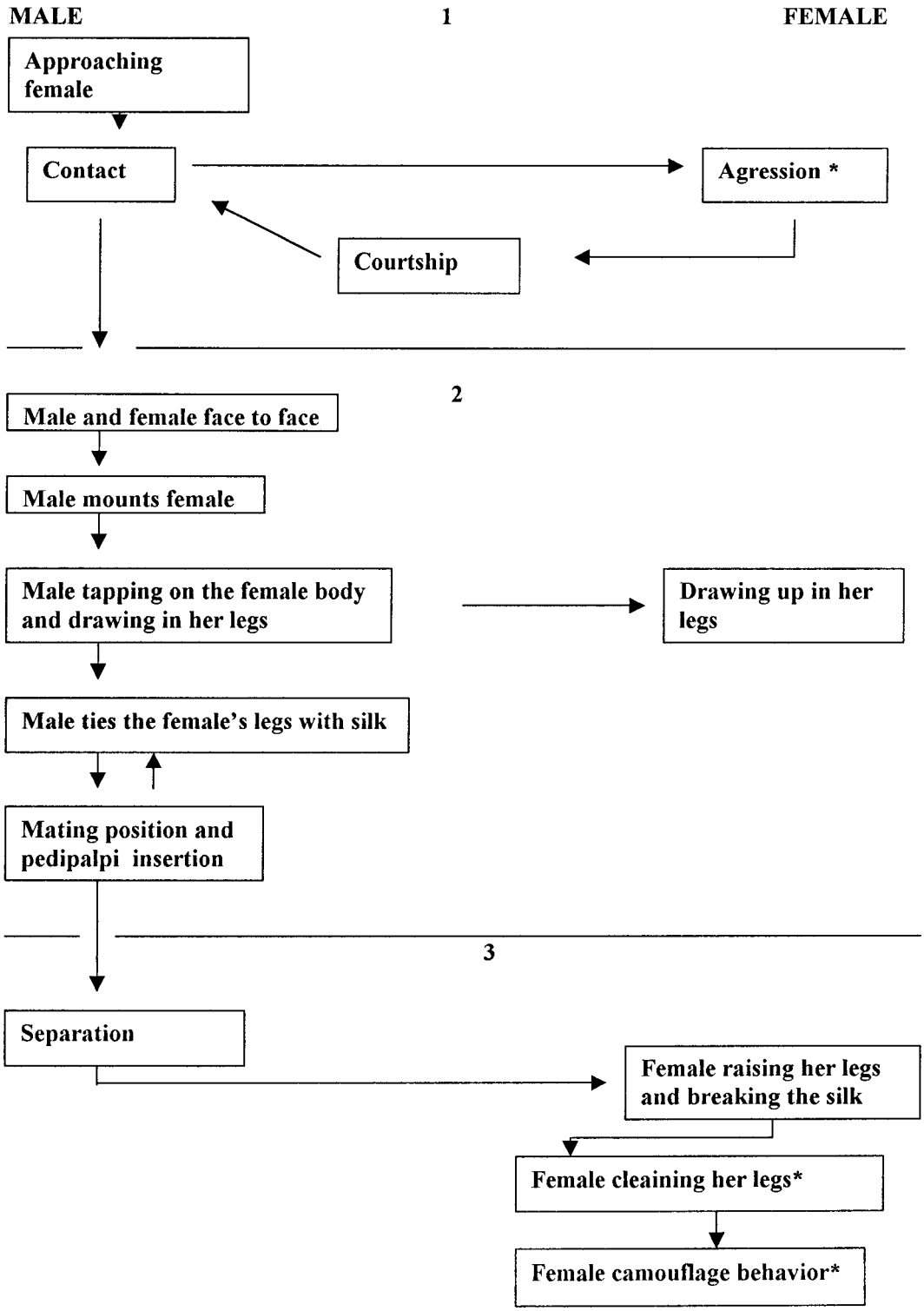
Adults and immatures were fed weekly with *Tenebrio molitor* L. larvae. The time during pre-oviposition, oviposition, number of egg sacs per female was recorded. Self-burying behavior was recorded for 27 recently molted spiders. These observations were recorded once with an RCA CCD video camera, with a 24x200m 100x eyepiece in natural light, and photographs were taken with a MINOLTA Dynax 8000i camera.

RESULTS

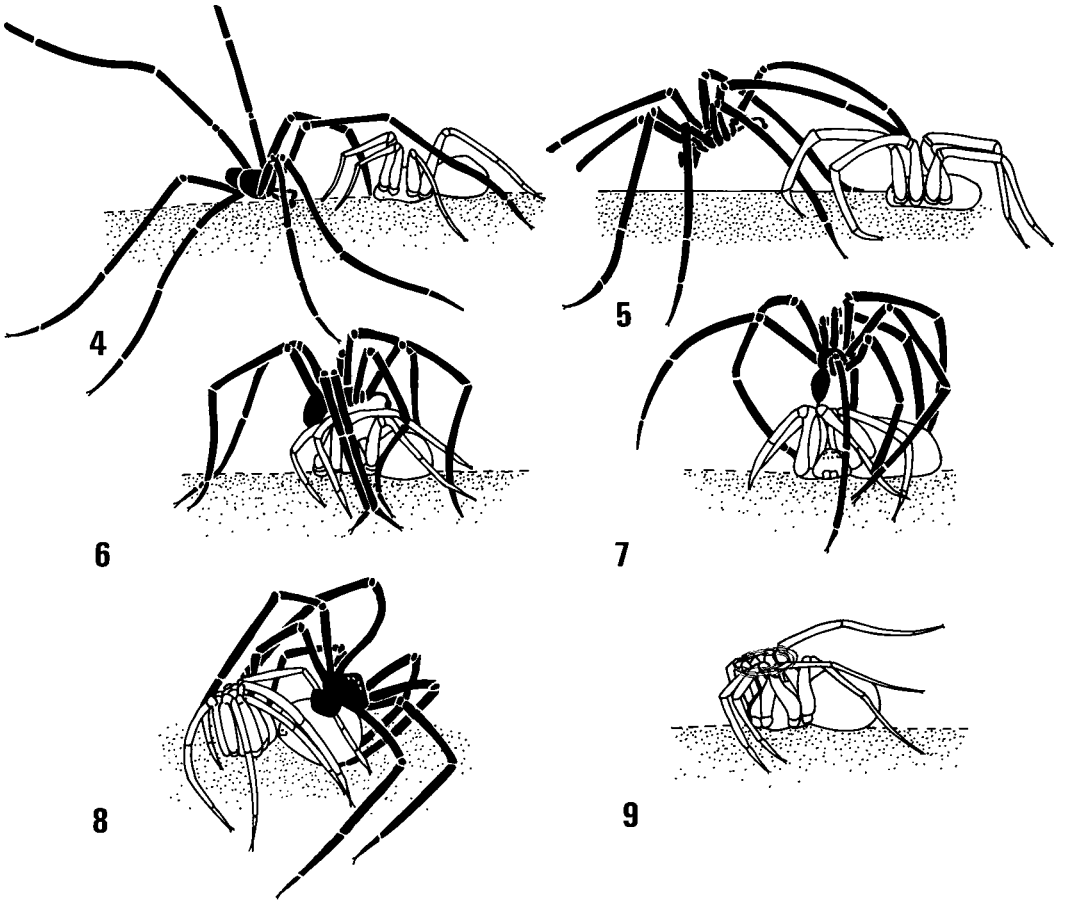
Field observations.—In both localities, 94% (n = 385) of the spiders were found under sections of fallen *Pachycereus pringlei* cacti, from 5 × 3 cm to 250 × 30 cm of size. Two percent (n = 9) of spiders were found under dead tree trunks, 2% (n = 7) under cartons, and 2% (n = 8) in crevices between cacti. Eighty-four percent of the spiders were found alone, 12% were grouped in pairs; and 3% were in threes. Of all spiders, 97% were found on the sand under cacti, 2% burrowing in soil and only 1% were observed in the paired leg formation. All captured spiders were found camouflaged with sand grains. At El Comitán sub-adults and females of *H. theologus* were present in October and November, whereas immatures were active all year and maintained an almost constant population size.

Mating behavior.—Courtship and mating behaviors of eight pairs of adult spiders were observed (8 males, 5 females were matured in the laboratory and then mated, 3 females of unknown mating status were captured in the field.). Sperm induction by males was not observed, but small triangular webs were attached to the jar walls indicated probable filling of palps with sperm. Sexual behavior was divided in to three stages: pre-copulation, copulation and post-copulation (Figs. 1–3).

Pre-copulation: The male approaches the female (Fig. 4), drums his palpi in an alternating sequence and attemps to mount her. If the female is not receptive, she attackes him (Fig. 1). Then the male courts by moving his



Figures 1–3.—Mating behavior of *Homalonychus theologus*. 1. Pre-copulation behavior. 2. Copulation behavior. 3. Post- copulation behavior. Asterisk means behavior observed only in some individuals (see text).



Figures 4–9.—Mating behavior of *Homalonychus theologus*. 4. M ale approaching to female. 5. Male tapping palpi and front legs on female's body. 6. Male drawing female's legs above her carapace. 7. Frontal view of male circling female's legs with silk. 8. Male and female mating. 9. Lateral view of female with the silk circle after mating.

front pairs of legs alternately up and down tapping the substratum, walking a few steps and stopping. The male repeats the sequence several times until he stands again in front of the female. This behavior was observed in only two males. Mean approach time was 11.3 min ± 23.6 (range 0–68.4 min, $n = 8$).

Copulation: When the female was receptive, she remained motionless on the substratum (Fig. 5) while the male mounted her, tapping his palpi on her carapace and tapping his front pairs of legs on her abdomen. During this process, the female adopted a passive posture, drawing her legs in close to her body so that the patellae of her legs almost touched one another above her carapace while the male helped her to maintain this position with his third pair of legs, resting only his fourth pair of legs on the substratum (Fig. 6). He immediately began spinning silk threads in a ring around the patellae and tibiae of the female to keep them together (Fig. 7). When she was well tied, the male leaned to the right or left side of the female for the mating position (Figs. 3, 8). The left palp was inserted in the left side ($\bar{x}$ 1.5, SD ± 1.2), and the right palp in the right side ($\bar{x}$ 2.6, SD ± 2.3) alternately several times. With each insertion, the male produced fast vibrations with the second and third pairs of legs. He added more silk threads to the ring, mated again and repeated the behavior. Mating lasted approximately 3.6 min (range 0.5–13.3 min, $n = 8$).

Post-copulation: After mating, the male ran

away rapidly and the female remained motionless for few seconds on the substrate (Fig. 9) suddenly breaking the silk circle, raising and extending her legs. Six of the 8 females cleaned the silk from their legs and rubbed them together. After mating, two females displayed the self-burying behavior, which is described later. Only two males tried mating again with mated females and only one of these was successful.

Of eight mated females, only two made egg sacs. The process was observed once. One egg sac was constructed under a fragment of cactus on the day following mating. The other was attached to the wall of a jar eleven days after mating.

Egg sac construction.—One female spun a silk sheet on the lateral wall of the container. After that, she attached silk threads with sand grains like ''collars'', made by moving her spinnerets from side to side on the substratum secreting silk to affixed small sand grains added to the spinnerets and then onto the silk sheet. She repeated this behavior to make the upper wall of the egg sac taking the form of a dome. Then she held herself with her two front pairs of legs to the inner wall of the dome, standing in a vertical position. In this position she continued making silk collars with sand grains, then she stopped this behavior and with the sand collars attached to her spinnerets, and still in vertical position she pushed herself to the top of dome adhering the sand collars in the outer wall, secreting silk threads to strengthen it. From time to time the female scratched in the sand on the bottom of the container, throwing sand grains with her two front pairs of legs and continued making collars, repeating the behavior described previously. Although it could not be seen how the egg sac was finished, this behavior was repeated until an opening in the lower rim was left, where she entered and covered the inside with silk. After 34 hrs the egg sac was finished, and the female deposited eggs for 30 minutes. She remained inside 13.5 hours more; then came out and closed the opening of the egg sac. The emergence of the immatures three months later was not observed. When the egg sacs were opened, one of them was empty and the other had 29 desiccated eggs.

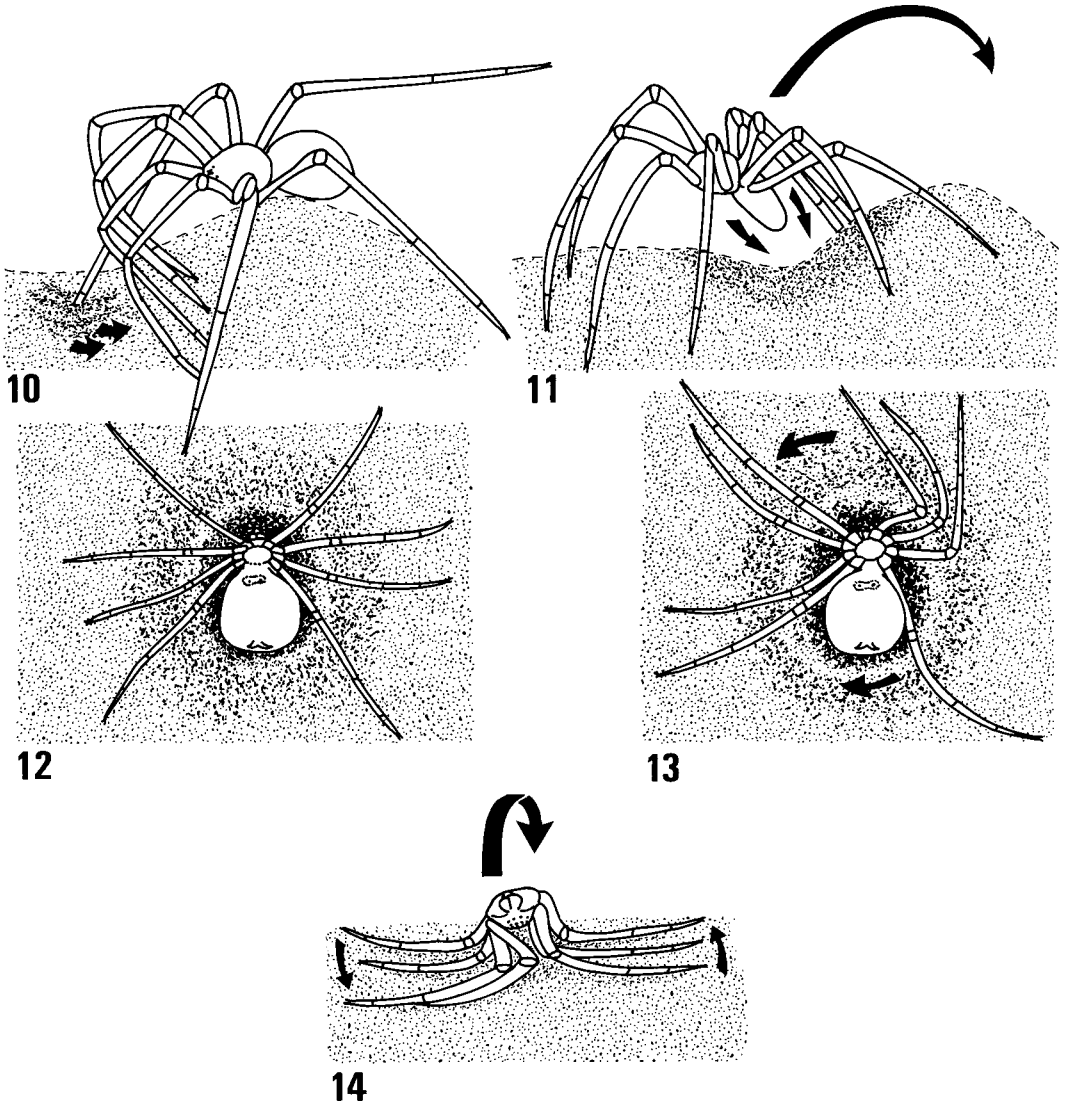
Self-burying and possible defensive behavior.—Under laboratory conditions observations were recorded on 27 recently molted spiders. To cover their bodies with sand, spiders scratched in the sand substrate with their palpi and first two pairs of legs, throwing sand grains from underneath the abdomen and making a small cavity (Fig. 10). They jumped and put their abdomen inside the cavity (Fig. 11). With their bodies in a vertical position, the spiders lay down on the sand mound with their ventral side up (Fig. 12). In this position, the spiders rocked their bodies slowly and continuously from side to side (Fig. 13). Then they flexed all their legs back and shook them from the patellae to the tarsi (Fig. 14). Finally they jumped up and in dorsal position placed their bodies on one side and extended the legs of the opposite side, shaking them rapidly back and forth in the sand. They scratched the sand substrate and repeated the behavior. Finally they expanded all their legs on the other side of their bodies and stood up totally covered with sand. Each spider performed this behavior twice (n = 26) with one spider performing it 7 times. This behavior was observed from the fourth instar to adult with the exception of adult males.

In captivity, almost all spiders of every instar burrowed in the soil. This behavior is different from described above and was recorded once as follows: The spider scratched in the sand with her two front pairs of legs, making a cavity. Then she jumped down and covered herself, throwing sand with her fourth pair of legs until completely buried. Then she extended her legs, moving them back and forth until they were outstretched and completely covered with sand.

Quiescent spiders and those collected in the field placed their legs in a rigid paired formation: the first two pairs forward and the last two pair backward, giving the appearance of dead cactus spines, according to Vetter & Cokendolpher (2000). When a spider was held by the leg with a pair of forceps, it rapidly autotomized the leg.

DISCUSSION

Field observations.—In San Pedro and El Comitan, spiders were found mainly under dead fallen cacti because rocks and stones are scarce in these habitats. In similar habitats *H. theologus* has been found under big rocks, loose boulders, boards and detritus (Roth 1984); but Vetter & Cokendolpher (2000) re-



Figures 10–14.—Self-burying behavior of *Homalonychus theologus*. 10. Lateral view of *H. theologus* scratching in the sand, forming a mound. 11. Lateral view of *H. theologus* putting its abdomen in the cavity. 12. Upper view of *H. theologus* with her ventral body up on the sand mound. 13. Upper view of *H. theologus* rocking its body from side to side on the sand mound. 14. Frontal view of *H. theologus* flexing her legs back and shaking them up and down in the sand. Arrows indicate the movements of *H. theologus* legs and body on the sand surface.

ported that the spiders were very scarce during daytime and speculated that they spend the daytime in rodent burrows and under rocks.

Mating behavior.—Sperm web structure of *H. theologus* males was similar to that described by Foelix (1996). When males were ready to reproduce, they rested on the substratum the container, presumablely searching for females; if they were not ready to mate, they remained suspended at the top of the container.

Homalonychus theologus courts at level I according to the classification of Platnick (1971) because it requires direct contact between male and female, but the courtship level could be between I and II because like lycosids, pisaurids and sicariids, the male of *H. theologus* probably detects the female by

some type of chemical stimulus, but this could not be verified in this study. The mating position of this species is a modification of type III position used by most hunting spiders, such as pisaurids, lycosids and thomisids (Foelix 1996). The male behavior of tying the female with strands of silk before or during mating has been recorded in other spiders such as the thomisid *Xysticus*, the philodromid *Tibellus* (Platnick 1971), the theridiid *Latrodectus* (Stern & Kullmann 1981), the dictynid *Dictyna* (Starr 1988) and the oxyopid *Oxyopes* (Preston-Mafham 1999). Similar bonds also are used by tetragnathid *Nephila maculata* (Fabricius 1793): the male places threads among the legs, the base of the abdomen and the carapace of the female (Robinson & Robinson 1980). The mating position assumed by *H. theologus* is very similar to that of the pisaurid *Ancylometes bogotensis* (Keyserling 1877) (Merrett 1988) in that the female's legs are trussed up tightly over the carapace. The male of *A. bogotensis* spins two silk rings, an outer ring around the distal ends of the front tibiae and an inner ring around the patellae (Merrett 1988). In the pisaurid *Pisaurina mira* (Walckenaer 1837), the male spins threads only between legs I and II of the female (Bruce & Carico 1988). Probably the male ties the female with silk to supress predation by the female during mating as has been the most consistent suggestion, although Foelix (1996) states that this behavior has symbolic significance only. Nevertheless Preston-Mafham (1999) suggests that producing the wrapping by the male is an important behavior and it seems highly likely that the silk plays a principal role in preparing the female physiologically and behaviorally for copulation. Post copulation behavior of the *H. theologus* female was similar to that observed in *A. bogotensis*, in which the female releases herself and cleans the silk from her legs (Merrett 1988).

Considering that courtship and mating behavior is an important phylogenetic character, it is possible that *H. theologus* is closely related to Pisauridae species, because the males of both tie the female with silk threads prior to copulation. Previously Homalonychidae was included in Pisauroidea (Lehtinen 1967) because they share some morphological characteristics with Oxyopidae and Pisauridae, such as eye pattern, feathery hairs, notched trochanters, and basic appearances of male and female genitalia. Nevertheless Roth (1984) argued to retain the Homalonychidae as a separate family because those characteristics are insufficient as justification to include this family in the Pisauroidea. Later Coddington & Levi (1991) grouped Oxyopidae, Pisauridae and Lycosidae, which share synapomorphies of male palp structure with other families in the super family Lycosoidea. We think that although homalonychid spiders have been isolated and restricted to the arid zones of the southwest USA and northwest of Mexico, its reproductive biology, genitalia and other morphological characteristics indicate a relationship with this family and therefore could be included in the super family Lycosoidea proposed by Coddington & Levi (1991).

Egg sac construction.—There are parallels among aspects of the behavior of *H. theologus* and the sicariid *Sicarius peruensis* (Keyserling 1880) because both are predominantly desert spiders. The construction of the *H. theologus* egg sac is similar to that of *S. peruensis* in that both species incorporate silk threads with sand grains. The size, form and texture of egg sacs are notably different between the species, as well as in the time for its construction and oviposition. It is interesting to point out that *S. peruensis* throws sand to bury the egg sac (Levi & Levi 1969), while *H. theologus* only attaches the eggsac to the substratum (Vetter & Cockendolpher 2000). This was verified in the field when an egg sac was found under a fallen dry cactus, and was so similar to the substratum that it was difficult to identify.

We agree with Vetter & Cokendolpher (2000) that it could serve to protect the eggsac against predators and parasites, but also to prevent it from desecation in the dry environment. During this study, none of the other females made egg sacs, but Vetter & Cokendolpher (2000) recorded two egg sacs per female. If our results and those of other authors are considered, females of *H. theologus* produce from 20–30 eggs per sac.

Self-burying and possible defensive behavior.—This behavior has been observed in other spiders such as *Sicarius* sp. (Sicaridae), but spiders of this species throw sand on the body when burrowing in the substratum (Reiskind 1965). Other spiders of the genera *Cryptothele* (Zodariidae), *Paratropis* (Paratro-

pididae), *Microstigmata* (Microstigmatidae), and *Bradystichus* (Bradystichidae) and the opilionid *Trogulus* (Trogulidae) have similar habits (Roth 1984). This behavior probably is an adaptation of these arachnids, including *H. theologus*, to protect themselves from predators although could it also serves as thermoregulatory function. This type of primary defense is of great importance in arid zones and deserts because there is relatively little vegetation cover to protect against predators (Cloudsley-Thompson 1996). The behaviors of leg autotomy and pairing of legs observed in *H. theologus* both belong to a secondary type of defense, effective when the spiders are threatened by predators (Cloudsley-Thompson 1995). Nevertheless *H. theologus* is mainly nocturnal like most other desert-dwelling spiders, therefore, a visual defense may be effective only in full moonlight, so sand camouflage could has obvious advantages however the leg pairing behaviour is more difficult to imagine functionally.

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